ASPECTS OF OXYGEN UPTAKE IN MESOCHAETOPTERUS TAYLORI, A TUBE-DWELLING POLYCHAETE ¹

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The genus *Mesochactopterus* was established by Potts (1914) and now includes five species (Hartman, 1959). The genotype *M. taylori* was collected by Potts at Nanaimo, British Columbia. Subsequent records and observations for this species include those of Berkeley (1922a, 1922b, 1930), MacGinitie and MacGinitie (1949), Ricketts and Calvin (1952), Berkeley and Berkeley (1953) and Barnes (1965). The significance of some of the experiments in the present investigation will be clarified by a brief account of the ecology of this animal. A more comprehensive treatment of ecological aspects, including feeding behavior and tubebuilding, has been published earlier (Petersen, 1966).

During the autumn of 1965 the authors collected more than 40 specimens of M. taylori, at False Bay on San Juan Island in Washington State. At False Bay the animals seem to be restricted to the zone from the middle of the beach to the lowest tidemark. However, it is possible that the population extends into the sub-tidal region as noticed by Potts (1914) at Nanoose Bay, where animals were dredged in 2 to 3 fathoms of water. M. taylori inhabits a very long tube, about 0.6 cm. in diameter. The tube projects from 0.5 to 2 cm. above the substrate and extends in a generally straight course to a depth of more than one meter. The tube is composed of an outer layer of sand grains adhering to an inner secreted organic lining. In large tubes the sand grain layer is often inconspicuous and the secreted layer has a parchment-like texture similar to the tube of *Chaetopterus* (Barnes, 1965). Potts (1914) states that a whole undamaged tube was obtained and that it ended blindly in a neatly rounded apex. Fine parchment-like tubes coated externally with sand were secreted by our animals which were kept in glass tubes open at both ends and oriented vertically in sand under running sea water. The lower ends of the secreted tubes were invariably rounded and closed.

In nature the upper end of the tube projects up to 2 cm. above the substrate, a fact that offers protection aganist predation and prevents the entrance of sand and coarse debris into the tube. It will also keep the tube water isolated from trapped surface water at low tide.

Considerable difficulty in digging up intact specimens and tubes has been mentioned by several authors. We attained a certain success by thrusting a spade with a long blade rapidly and vertically into the sand about 6–8 cm. from the protruding

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end of the tube. After reaching a depth of more than 30 cm. the point of the blade was moved towards the tube to immobilize the animal by compression against the tube wall. The spade with animal and tube was then carefully removed. In the case of broken specimens the remainder of the animal was usually recovered by subsequent digging.

The experimental part of the present investigation concerns the measurement of oxygen uptake in *M. taylori* at various levels of external oxygen tension. In addition, measurements were made of changes in oxygen availability inside the tube during intertidal exposure. Differences in oxygen tension between interstitial water and tube water were assessed and provided information on the diffusion properties of the tube material. The latter point was also directly tested in the laboratory by changing the oxygen tension across tube wall material while monitoring the rate of oxygen transfer.

METHODS AND EXPERIMENTAL PROCEDURE

Field sampling

Samples of interstitial water were obtained in close proximity to the tube from which water samples were taken. An aluminum pipe with a cone-shaped end and an inner metal plunger was forced into the sand to the desired depth. By lifting the plunger the interstitial water was drained into the pipe through a series of small holes. Mineral oil applied between the plunger and the pipe prevented contamination of this water by gases in the atmospheric air. A thin stainless steel cammula was used to sample the water from the enclosed compartment at the end of the pipe. The water samples (0.5 to 1.0 ml.) were obtained at depths ranging from 5 to 30 cm. The samples were analyzed for oxygen tension shortly after they were obtained, using a Beckman Spinco Gas Analyzer (model 160).

Water samples from inside inhabited tubes were taken at 20–40-minute intervals throughout the tidal cycle, starting just before the water subsided and continuing until the water again covered the top of the tubes. These samples were obtained by carefully inserting a thin stainless steel cannula into the tube. After filling the dead space with tube water, the samples (1-2 ml.) were drawn into glass syringes which were subsequently sealed and brought to the laboratory for immediate analysis. The samples were taken from various depths in the tubes (5-30 cm.). All gas analyses were done at 10° C, which corresponded closely with the temperature prevailing in the normal environment.

Laboratory experiments

The oxygen consumption (VO_2) of *M. taylori* was measured in a closed system using an oxygen electrode as a continuous sensor of the oxygen pressure in the metabolism chamber. The oxygen uptake was determined at various levels of PO_2 as the animals reduced the oxygen pressure in the chamber through their own respiratory activities. The volume of the metabolism chamber was selected in the approximate range of the water volume (30–40 ml.) calculated to be present inside a normal tube. The wet and dry weights of the animals were carefully recorded. Oxygen consumption was expressed as ml. O_2/kg . dry weight/hour. The diffusibility of oxygen and permeability of water through tube wall material was tested in the following way: A section of an intact tube (15 cm. long) was closed at one end and placed vertically in sea water of 10° C. An oxygen electrode was carefully inserted into the tube compartment and another electrode was placed in the water compartment surrounding the tube. The output from the 2 electrodes was continuously monitored when nitrogen or pure oxygen was bubbled in the surrounding water or in the water phase inside the tube. The rate of change of oxygen tension inside and outside the tube provided the needed information to evaluate the diffusibility of oxygen through the tube wall. The permeability to water was simply assessed by filling one or the other of the compartments described above with sea water and observing any changes in water level.

RESULTS

The interstitial water samples were uniformly low in oxygen tension averaging from 5–8 mm. Hg and invariably less than 12 mm. Hg. No significant relation to depth or phase of outgoing tide was detected. The oxygen tension in the tube water ranged between 70–110 mm. Hg just before the beginning of ebb. Oxygen tension in the surface water covering the sand flats just before exposure during outgoing tide ranged from 130 to 150 mm. Hg, while stagnant trapped pools containing lots of organic material showed a much reduced oxygen tension, at times below 100 mm. Hg. The oxygen tension in tube water declined steadily throughout



FIGURE 1. Hatched area: Decline of tube water PO₂ during tidal exposure. Start of tidal exposure at time zero. Plotted lines: Rate of PO₂ change in the closed metabolism chambers.

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FIGURE 2. Oxygen uptake (ml. O_2/kg . dry weight/hour) plotted against oxygen tension in the ambient water.

the tidal exposure and reached values ranging from 16–30 mm. Hg at the end of exposure periods lasting from 2 to 3 hours.

Figure 1 depicts the average decline in oxygen tension of the tube water (hatched area) plotted as log PO_2 against time. In spite of considerable scatter, due mainly to differences in burrow size and animal size, the values attested to a clear linear regression. The course of the oxygen tension decrease inside the metabolism chambers used in the laboratory experiments (plotted curves) is also shown in Figure 1. Here again there is a set of linear regressions but with varying slopes depending on the size of the animals. The volume of water and animal combined was constant in all experiments and within the range of that occurring in natural tubes. Figure 1 indicates that there must be a linear relationship between oxygen uptake and oxygen tension in the surrounding water. This phenomenon is more specifically expressed in Figure 2 which shows a composite plot of oxygen uptake *versus* oxygen tension in the surrounding water within a range in PO_2 from 110–5 mm. Hg. Figure 1 also points out the importance of the tube wall as a diffusion barrier in as much as the decline of PO_2 was only influenced by the oxygen uptake rate of the animal and not by the steep gradients in oxygen tension shown to be

present across the tubes in nature. No significant exchange of gases or water could hence have occurred between the interstitial and tube water compartments. This was substantiated by the experiments designed to directly study the diffusion properties of the tube wall material. These experiments revealed the tube to be virtually impermeable to water and to oxygen within the gradients found to be present under natural conditions.

DISCUSSION

Evaluation of tolerance to oxygen deficiency in intertidal polychaetes requires consideration of a number of factors such as oxygen uptake in relation to external oxygen availability and oxygen tension changes internally in tissues and body fluids. If a respiratory pigment is present, its concentration and respiratory properties, in addition to blood flow and oxygen content of circulating blood, would have to be assessed.

In *M. taylori* there is no respiratory pigment, and survival during tidal exposure will thus depend primarily on the relationship of oxygen consumption to oxygen availability. The present results (Figs. 1 and 2) reveal a steady reduction in oxygen uptake as the surrounding PO₂ goes down. VO_2 dropped to $\frac{1}{4}$ of the original value when the surrounding PO₂ changed from 100 to 10 mm. Hg. This phenomenon, usually referred to as respiratory dependence, can depend either passively on the reduced external oxygen availability (Van Dam, 1938) or on active changes in the respiratory gas exchange of the animal (Johansen and Vadas, 1967). In order to ascertain whether the latter possibility is operating it is necessary to monitor both external (surrounding water) and internal oxygen tensions simultaneously. Such an approach was unfortunately not technically feasible with *M. taylori*.

The present finding that the PO_2 decline in the metabolism chambers closely resembled those recorded from normal tubes during an average 3-hour tidal exposure indicates that the animals must virtually exhaust their oxygen supply during low tide. The apparent limitation in the distribution of these organisms to the outer region of the intertidal zone may have evolved in response to the limited oxygen supply in the tubes.

On the other hand the results attest to a crucial role of the tube in the survival and distribution of the animal. That is, the tube wall material represents a protective diffusion barrier between the almost anoxic interstitial water and the water inside the tubes. It seems appropriate to emphasize this role as an important survival factor for a sedentary tubiculous polychaete living in an anoxic substrate. The fact that the tube of M. taylori is closed at the lower end is essential for the protection offered by the tube wall.

In discussions of adaptive significance related to tubiculous life, protection from predators and possibilities for specialized feeding mechanisms have often been pointed out (Nicol, 1960). However, the biological significance of the diffusion barrier represented by the tube wall, as demonstrated in the present work, appears never to have been appreciated earlier. It would be of interest to know how common this characteristic is among sedentary tubiculous polychaetes. Errant inter-tidal polychaetes certainly do not enjoy the same protective confinement from the commonly very anoxic conditions of the intertidal substrate (Jones, 1955).

SUMMARY

1. Oxygen uptake, \dot{VO}_2 , in *M. taylori* has been studied as a function of external oxygen availability. VO, dropped linearly as external PO, declined.

2. The rate of PO₂ decline inside normal tubes of M. taylori during tidal exposure indicates that the oxygen supply is nearly exhausted during an average 3-hour tidal exposure.

3. A comparison of oxygen tensions in interstitial water and tube water during tidal exposure revealed that the tube is impermeable to water and oxygen. This finding was confirmed by direct laboratory experiments.

4. The distribution and survival of M. taylori are discussed in relation to the results obtained.

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